THE EFFECTS OF ANIMAL ACTIVITY IN THE LITTER LAYER

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THE EFFECTS of animal activity in woodland litter can often be more readily determined than the animals themselves. Holes made in leaf tissue, frequently accompanied by accumulations of excrement, can be easily seen with the naked eye. A ten- or twenty-fold magnification clearly shows that smaller animals also attack the dead leaf and leave behind their feeding patterns and droppings. But the direct attack on the leaf tissue is only one, albeit a very important, aspect of animal activity in the litter layer.

In general, it can be stated that the animals living in and on litter influence their environment by their movement and feeding habits. As they move they shift both organic and inorganic material (transportation), and they also affect the distribution of microorganisms (inoculation). As the litter fauna feeds, it may give rise to a physical and chemical attack on the litter (fragmentation and digestion), but feeding may also result in removal of microorganisms (sanitation).

Excrement deposition

The earthworm, *Lumbricus terrestris* L., is an example of an animal which transports litter in a spectacular manner. It lives in burrows of 1–2 m depth, and without altogether leaving its burrow it pulls leaves into it from round about and devours them on the spot. Other species, such as *L. rubellus* (Hoffm.) and *Dendrobaena octaëdra* (Sav.), which live more on the surface and largely feed in the litter layer, add some inorganic material to this layer as they deposit their casts between the leaves, but add organic material to the upper soil layer as they cast in their superficial burrows. Enchytraeids may also form such burrows, although on a much smaller scale.

Many litter-inhabiting animals are comparatively immobile and consequently cause local accumulations of excrement next to their

source of nourishment. Such are Lycoriidae, Phthiracaridae and Enchytraeidae. Others are continually shifting, so that their droppings are scattered, sometimes at a considerable distance from their food, e.g. Diplopoda, Isopoda, Tipulidae, Collembola and several Orbatei.

Effects on microorganisms

Although the effect of movement and feeding habits on microorganisms is undoubtedly very important, a great deal of work has still to be done in this field. Animals inhabiting the litter layer can, of course, be continually infected with spores of microorganisms which they lose during their travels. An animal placed on a sterile nutrient medium causes the development of bacterial, and frequently also fungal, colonies. Under natural conditions this development will obviously also occur when the nutrient substrate, humidity, pH, etc., are favourable (inoculation). Most litter animals feed on dead foliage, so absorbing countless numbers of microorganisms. Other species prefer fungi or bacterial colonies as such. Not all bacterial and fungal cells ingested in the gut are attacked. The survivors may develop into new colonies when they find a suitable habitat. When a collembolan species, *Onychiurus quadriocellatus* Gisin, was fed on a sporulating colony of *Cladosporium* sp., it produced droppings entirely consisting of hyphae and spores. When placed on a suitable agar plate the hyphae failed to develop, and only 13 per cent of the visually undamaged spores germinated. Under the same conditions, 83 per cent of the fresh spores germinated.

A suitable substrate is required for the development of microorganisms transported by animals. It seems likely that the feeding activity itself produces suitable locations, for the plant tissues exposed by the feeding process create an entry for attack by microorganisms from which they are able to penetrate into the inner cell layers. The droppings, which in most cases consist of finely divided vegetable matter, may form nuclei favourable to the development of bacterial or fungal growth and may in the latter case soon be covered with a dense layer of sporophores. This situation maintains itself until the next function of the litter fauna, i.e. sanitation, can be performed by some mycophagous type of animal (Staphylinidae, Diptera larvae, Collembola, Oribatei). Sporophores and hyphae are stripped off, and the components of the pellets are separated out, thus facilitating attack by the next microorganism or group of organisms. This will also exhaust its food resources, and when the colony is fully developed it has to make way for the organism best adapted to the new situation.

Protozoa, Nematoda, Collembola and Enchytraeidae are important agents in the clearance of bacterial colonies.

Feeding activities

The feeding activity of animals can probably best be outlined by following the attacks made by animals on a newly fallen leaf. Microbiologists have found that leaves are attacked by microorganisms even before they fall. Some of these organisms continue to live in the leaf after it reaches the ground, while others disappear and are succeeded by other species (Burges, 1963). This first attack by microorganisms is probably very important for the subsequent attack by the fauna. An equally important factor is the flushing of the leaf by rainwater. Tardigrada, Rotifera and especially Nematoda are encountered in large numbers on places with free water between the leaves. This 'water fauna' mainly feeds on microorganisms in the film of moisture. Also Collembola, Oribatei and Enchytraeidae are found on the newly fallen leaf. They strip the microvegetation from the leaf surface (mainly algae and fungi), leaving behind their fairly uncharacteristic droppings. Up to this point there is scarcely any attack on the leaf tissue.

The attack begins after a few weeks or months, depending on the type of leaf. Leaves with soft, thin-walled tissues are attacked readily (alder, elm, hazel, etc.), others with thick cuticula and cell walls are despised (oak, beech, coniferous trees). Thin shadow leaves are attacked earlier than thick sun leaves. In the initial phase various species of snails devour large pieces, but millipedes, isopods and dipterous larvae also begin to eat the leaf. With the arthropods the feeding pattern is rather uncharacteristic. Related species occasionally avoid the leaf veins in varying degrees, thus producing different feeding patterns, but the differences within the same species are often still greater, depending on the size of the animal. To a certain extent the droppings are characteristic of particular groups, although there may be differences in the size, colour and shape of the pellets even of the same animal, depending on the type and character of the food.

As the leaf ages, the micro-arthropods and enchytraeids settle on it in greater numbers and diversity of species. They forage on the leaf, which has now become softer, and form small feeding patches. The Collembola in particular feed on the droppings of other animals and these droppings are reduced still further as a result. Both Oribatei and Collembola feed on the fungal hyphae and sporophores. Collembola leave behind black patches or small pellets, depending on the moisture content and the type of food. Oribatei droppings have

a more or less oval shape. Enchytraeids deposit fairly large masses of amorphous excrement, preferably along projecting veins.

Detritus

An increasing amount of fine detritus is now gradually formed in the decaying foliage and harbours various kinds of microorganisms. In addition to bacteria and fungi, this detritus also houses the camoeba, rotifers, tardigrada and nematodes which develop so long as the moisture content is sufficiently high. When the mass of detritus becomes desiccated, its inhabitants enter a state of anabiosis and do not revive until moist conditions return. This mass of detritus can again be ingested by earthworms (*Dendrobaena* sp.), enchytraeids (*Cognettia* sp.) or collemboles (*Tullbergia* sp.), and once more deposited in the form of detritus after passing through the gut. A considerable amount of it is washed away by rain and deposited in the A_1 layer. All that is left of the leaf are now small fragments which have managed to escape attack and leaf veins which are slowly devoured by endophagous Phthiracaridae.

Speed of litter breakdown

The speed of the above-mentioned process of litter breakdown is greatly dependent on (1) the qualitative and quantitative composition of the soil community, (2) the composition of the litter layer and (3) the weather conditions influencing the activity of the soil organisms.

The qualitative composition of the soil fauna is determined by local environmental conditions as well as by geographical and historical factors. Without entering into a detailed discussion of the matter, it can be stated that important environmental features are the physical and chemical properties of the soil, the average and extreme levels of the water table, humidity, temperature and evaporation, the composition of the vegetation and the litter it produces. These factors determine the presence or absence of a species. The population density is determined by the interaction of all factors that may in any way influence the life processes of the species and its chances of survival. Great differences may occur in the soil fauna from year to year, often mainly owing to extreme weather conditions. Thus, during the very dry summer of 1959, *Enoicyla pusilla* Burm., the larvae of which are extremely sensitive to drought, was practically exterminated in many woodland areas, and there was also a marked decline in the numbers of other animal groups (Van der Drift, 1963).

Different kinds of litter are devoured by the fauna in extremely varying degree. Dunger (1962) has shown that all animal groups

investigated exhibited practically the same series of preferences. This series is substantially the same as the order in which litter disappears under natural conditions (Wittich, 1939, 1943). Factors which may be of influence in this connection are the mechanical properties of the leaf, moisture content, nitrogen content or C/N quotient and flavouring materials which may either be components of the leaf itself or the result of microbial activity (Dunger, 1958).

On carrying out preference tests with individual specimens of *Glomeris marginata* Vill., the author and his colleagues found that the previous food may influence the choice of diet and that there may also be marked individual differences in preference. Thus of three animals which had been fed for four days on alder litter, for which they generally show a distinct preference, and were then given a choice between alder, birch, oak and poplar, two continued to prefer alder but the third rejected it and showed a distinct preference for birch, of which the other two animals had, in fact, also eaten large amounts. After they had again been fed on alder for a fortnight and were given then the same choice, the first two animals now preferred poplar while the third again showed a predilection for birch. This is only an example from preliminary tests, which suggests that the preference for a given food is not so strong as the need for variety—a requirement which is always satisfied in nature. Field observations confirm this, because a preferred diet is never exhausted before a start is made on other litter.

In conclusion, weather conditions affect the rate at which the litter is converted. During a mild winter most of the animals continue their feeding activities, although the intensity is much lower than in the spring and feeding is periodically interrupted during cold spells. In Western Europe, from April onwards the temperature conditions are usually more conducive to animal activity, but owing to the lack of foliage in deciduous forests at this time, the litter layer may become so dry in sunny weather that the activity ceases. The most favourable period for the activity of the litter fauna is that in which the foliage is closed; this, together with a dense herb vegetation, prevents the litter layer from drying up. Usually the activity declines in the summer and revives again when the leaves fall in autumn, but this largely depends on the life cycle of many species.

Rate of breakdown

The ultimate effect of all these factors on the rate of litter breakdown is the complete or partial disappearance of the litter formed each year before the commencement of the next leaf fall. *Figure 1* shows the results of weighings of the entire litter layer in September (prior

to the leaf fall) and in December (after the leaf fall) in two adjoining woodland plots of a mull and a mor type. Positive and negative deviations from the 10-year temperature and precipitation averages are indicated. In the mull type, the litter has usually more or less disappeared by the next leaf fall or, with favourable weather conditions, even long before. Thus in the warm but wet year 1957, the

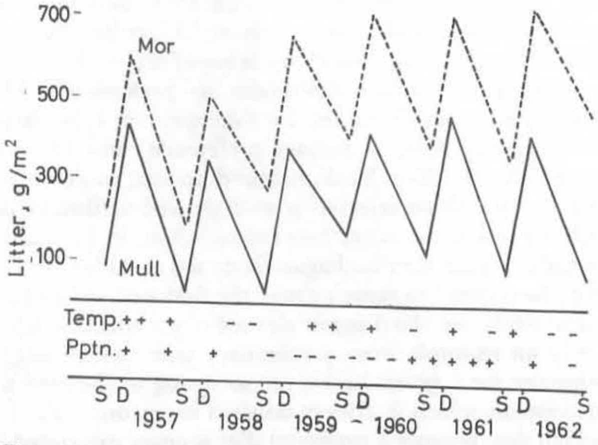

Figure 1. Weights of the entire litter layer in mull and mor part of deciduous woodplot, compared with rough deviations from 10-year temperature and precipitation averages

litter had practically disappeared as early as June. In the less favourable year 1958, the litter also disappeared except for a very slight residue, but in this case the entire season was required. In the exceptionally dry year 1959, decomposition was so slight that there was a considerable residue, but under the less unfavourable conditions of the subsequent years this accumulation was gradually reduced.

Mor and mull

Although litter is always left behind in the mor type, this does not mean that its annual breakdown is always less than in the mull type. Under the favourable conditions prevailing in 1957, more litter was broken down in the mor, as in this case the amount was not the limiting factor. Even in the unfavourable year 1959, decomposition was slightly greater than in the mull. Apparently the thick litter layer in the mor provided a better protection against drying than the thin litter layer in the mull. The arrears of decomposition in 1959 in

the mor could not be made good in subsequent years. The series of six years shows a clear tendency to accumulation in the mor type which is absent from the mull type.

Changes in the litter effected by the fauna

Let us finally consider the question of the changes which the fauna effects in the litter by its eating habits. Microscopic and microchemical examination of the faecal pellets of animals fed on a particular type of litter clearly shows that there is only a very slight degree of digestion and that the most important effect is the reduction of the litter to fragments which are combined into porous agglomerates. The faecal pellets of *Enoicyla* larvae contain an average of 3,000 particles of 60 μ diam. The surface exposed to attack is multiplied fifteen times, and there is a considerable increase in aeration and moisture retentivity. The pH is also slightly increased, possibly owing to ammonia secretion, and this also increases bacterial development, as reflected in a marked increase in the carbon dioxide production (Van der Drift and Witkamp, 1959). Since the microvegetation exhausts its nutrient medium, this CO_2 production returns to its original level in a few weeks. The attack cannot be renewed until the old colony has been removed.

There must, however, be some degree of digestion as the food passes through the gut. Careful weighing of food, food remnants and excrement of millipedes and isopods showed retention percentages of from 4 to 20 per cent. *Table 1* lists the amounts consumed and retained by the millipede *Chromatoiulus projectus* (Verh.) on litter from

Table 1

Average consumption and retention of eight females of *Chromatoiulus projectus*

Average living weight 193·5 mg; water content 220 per cent absolute-dry

Period	*Food*	*Consumption* mg dry wt./100 mg live wt./wk.	*Retention*	*Retention in* per cent *consumption*
14–21.3	Birch	3·1	0·50	16·2
21–28.3	Alder	8·4	1·69	20·2
28.3–4.4	Oak	3·7	0·42	11·2
11–18.4	Poplar	6·3	0·34	5·3
18.4–10.5	Hazel	21·9	1·77	8·1
14.6–15.8	Hazel	15·4	0·57	3·7

birch, alder, oak, poplar and hazel. It shows that hazel is by far the most popular food. It could be calculated from the number of pellets and the maximum gut contents that the gut was filled about five times a day. Direct observations of animals with changing food demonstrated a passage time of about 3 h. With such a rapid passage it is clear that digestion can only be superficial and, in fact, retention only amounts to 8 per cent of consumption. Alder litter shows the same absolute retention for a much lower consumption, the gut being filled only twice a day and retention amounting to 20 per cent. Consumption and retention are much lower in birch, oak and poplar, but the retention percentage is highest where consumption is lowest. Obviously, however, the digestion is also influenced by the type of food, and it would seem that alder is readily digested but that poplar, which is consumed in only a slightly lower amount, occasions difficulty. Finally, both the consumption and retention percentages show a marked decline when the diet is unchanged for a long continuous period.

Chemical examination of food and faecal material showed what components of the food are digested in different cases. In this connection it should be remembered that, owing to the selectivity of consumption, the composition of food consumed differs from both the food supplied and the residue. Bocock (1963) found that Glomeris had fairly high assimilation percentages for crude fats, soluble carbohydrates and even holocellulose, while Van der Drift and Witkamp (1959) found that, in Enoicyla, assimilation was practically confined to easily decomposable carbohydrates. Priesner (1961) was able to demonstrate by means of paper chromatography the assimilation of nitrogenous compounds by *Tipula maxima* Poda.

An entirely different approach to the problem of chemical attack of the litter by the fauna is the examination of the enzymes occurring in these animals. Overgaard Nielsen's (1962) recent study of some thirty soil animals makes it seem likely that only snails are capable of attacking cell-wall materials. Nevertheless the droppings of these animals also contain many fragments which are scarcely if at all attacked. It is probable that only the part absorbed in the hepatopancreas is subject to a sufficiently strong cellulase action. Its black colour and amorphous structure clearly distinguish it from the rest of the excrement and it is obviously far more highly digested than the other food. The exclusive presence of pectinase and xylanase in Tipulidae larvae may possibly be related to the caeca of these animals in which part of the food is absorbed and severely attacked. In this case, the enzymes in question would be derived from the symbiotic microorganisms in these appendices (Buchner, 1953). In this

connection it would also be important to examine the enzymes of other litter animals such as the larvae of Potosia and Geotrupes which have also provision for symbiotic organisms.

According to Nielsen, the food assimilated by litter fauna chiefly consists of the bacteria and fungi ingested with the vegetable material. As the writer sees it, the soluble carbohydrates and nitrogenous compounds of the cell contents remaining in the litter are also components in the diet. But it would seem fairly certain that this is relatively unimportant for the changes in the chemical composition of the litter. Its decomposition is almost entirely due to microorganisms, but for these to thrive, animal activity is essential. Experiments in which animals were excluded have shown this (Kurčeva, 1960).

The interrelations between litter fauna and microorganisms are a fascinating field of study for soil zoologists and soil microbiologists.

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